

Revision of the Protobranch Species Described by Dautzenberg & Fischer (1897) with Description of a New Species and Taxonomic Comments on *Bathyspinula* (Bivalvia, Nuculanoidea)

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Abstract. In 1897, Philippe Dautzenberg and Henry Fischer described six deep water protobranches from the North Atlantic (*Princesse-Alice* expeditions, 1894, 1896): *Leda excisa* (Philippi) var. *subexcisa*, *Leda bernardi*, *Leda allaudi*, *Leda mirmidina*, *Leda mabiliei* and *Malletia perrieri*. Almost all of these taxa are only known from the original description, with no further records in the modern literature. The present revision, based on the original material, led to the following combinations: *Bathyspinula subexcisa*, *Ledella bernardi*, *Yoldiella allaudi* (lectotype designated), *Microgloma mirmidina*, *Nuculana mabiliei* and *Tindaria perrieri*. A new species is described as *Yoldiella dautzenbergi* from material misidentified as *Leda allaudi*. Taxonomic comments are given for the genus *Bathyspinula* Filatova, 1958. The subfamily Bathyspinulinae Coan & Scott, 1997 (= Spinulinae Allen & Sanders, 1982 *nom. inval.*), formerly in the family Nuculanidae, is raised to full family rank within the Nuculanoidea. *Tindariopsis* Verrill & Bush, 1897 is also assigned to the Bathyspinulidae.

INTRODUCTION

Dautzenberg & Fischer (1897) described six new deep water protobranches from the North Atlantic (*Princesse-Alice* expeditions 1894, 1896): *Leda excisa* (Philippi) var. *subexcisa*, *Leda bernardi*, *Leda mabiliei*, *Leda allaudi*, *Leda mirmidina* and *Malletia perrieri*. Almost all of these taxa are only known from the original description, with no further records in the modern literature on the North Atlantic molluscs. A single species, *Spinula subexcisa* (Dautzenberg & Fischer, 1897), was included in two taxonomic works (Clarke, 1961; Allen & Sanders, 1982), but without examination of the type material. The present work offers a systematic revision of these poorly known species, based on the original material. This paper also gives an occasion to discuss the taxonomy of the genus *Bathyspinula* and its systematic position within the Nuculanoidea.

MATERIAL AND METHODS

The *Princesse-Alice* stations from which Dautzenberg & Fischer (1897) described the species dealt with in the present work are reported in Figure 1. Dautzenberg (1927) renumbered all the stations from the *Princesse-Alice*, *Hirondelle* and *Prince de Monaco* expeditions (1886–1913) as a single series, with longitudes west of Greenwich, whereas the original longitudes were west of Paris. In the present work, station numbers and longitudes are according to Dautzenberg's (1927) list,

with the original station number in parenthesis. Dautzenberg (1927) also reported the same descriptions and illustrations as those originally published by Dautzenberg & Fischer (1897).

The type material is from the Musée Oceanographique de Monaco, the Institut Royal des Sciences Naturelles de Belgique, Bruxelles and the Monterosato collection, Museo Civico di Zoologia, Rome. A list of this material is reported in Table 1.

The nuculanid classification adopted in the present work follows the scheme by Ockelmann & Warén (1998), except for the position of the genus *Bathyspinula*.

The following abbreviations are used: exp(s) – expedition(s), sh(s) – complete shell(s), paired valves; v(s) – valve(s); IRScN – Institut Royal des Sciences Naturelles de Belgique, Bruxelles; MOM – Musée Oceanographique de Monaco, MCZ – Museum of Comparative Zoology, Harvard University, Cambridge, MZR – Museo Civico di Zoologia, Rome.

SYSTEMATICS

Family Nuculanidae H. & A. Adams, 1858

Genus *Nuculana* Link, 1807

Nuculana mabiliei (Dautzenberg & Fischer, 1897)

(Figures 2a–e)

Leda mabiliei Dautzenberg & Fischer, 1897:207, pl. 6, figs 9, 10.

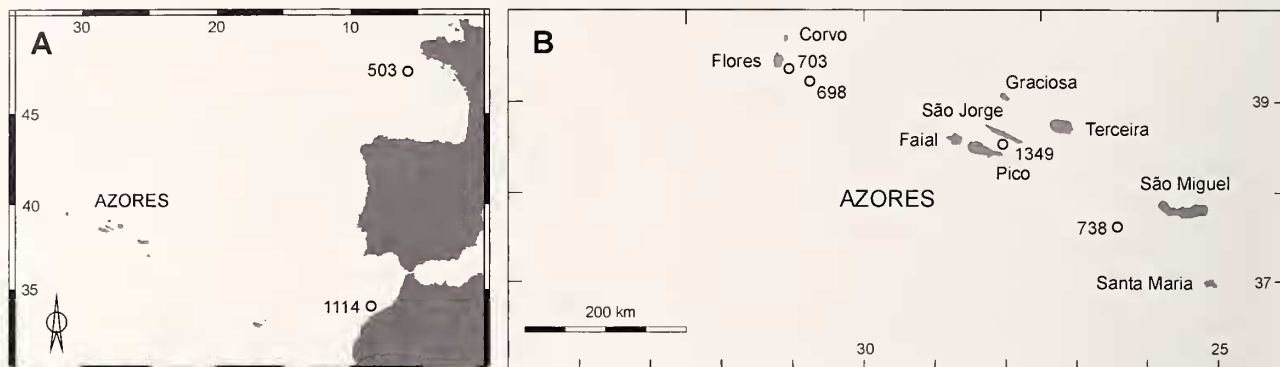


Figure 1. Monaco expeditions, stations 503, 698, 703, 738, 1114, 1349.

Leda mabiliei – Dautzenberg, 1927:291, pl. 8, figs 25, 26.

Types: Monaco exps., st. 503 (*Princesse-Alice* 1894, st. 101), 47°10'N, 5°47'45"W, 748–1262 m, 1 v, MOM 21160, holotype.

Distribution: Only known from a single deep water station off the Bay of Biscay.

Remarks: The single, poorly preserved type right valve is notably robust and convex, triangular-elongate in shape, with a short, truncate, bicarinate rostrum and a wide, slightly concave postero-dorsal area. The sculpture consists of commarginal ridges, somewhat irregular in spacing and strength, slightly coarser posteriorly (Figures 2a, d). The hinge is relatively strong, with a triangular, oblique ligament pit (Figure 2e). A shallow, poorly defined rostral ridge is present internally. The rostrum tip is slightly broken (Figure 2d), giving appearance of an oblique truncation, as in the original description (*rostrum oblique truncatum*).

Leda mabiliei can be easily assigned to the genus *Nuculana*. It is different in many respects from the two well known North Atlantic species of *Nuculana*, i. e. *N. pernula* (O.F. Müller, 1776) and *N. minuta* (O.F. Müller, 1776). Good illustrations of these two species were reported by Schiøtte & Warén (1992). Due to the short rostrum, *Nuculana mabiliei* is more similar to *N.*

minuta, from which it differs mainly by being less elongate and more triangular in shape, more robust and convex.

The occurrence of *N. mabiliei* in a deep water station is puzzling, as species of this genus typically occur in shallow waters. Moreover, this species is notably different from some deep water nuculanids with a long, slender and bent rostrum which can be assigned to *Thestyloda* Iredale, 1929 (Di Geronimo & La Perna, 1997). The valve of *N. mabiliei* could have undergone a down-slope transport from outer shelf bottoms, as also suggested by its poor preservation status.

Genus *Ledella* Verrill & Bush, 1897

Ledella bernardi (Dautzenberg & Fischer, 1897)

(Figures 3a–f)

Leda bernardi Dautzenberg & Fischer, 1897:206, pl. 6, figs 5, 6.

Leda bernardi – Dautzenberg, 1927:289, pl. 8, figs 21, 22.

Nuculana bernardi – Clarke, 1962:52.

Types: Monaco exps., st. 738 (*Princesse-Alice* 1896, st. 109), 37°40'N, 26°25'15"W, 1919 m, 1 v, MOM 21158, holotype. Same station as holotype, 2 vs, IRScN 1238/5.

Distribution: Only known from a single deep water station, west of São Miguel, Azores.

Remarks: *Leda bernardi* was described from a single right valve (MOM) (Figures 3a–c), but two other valves from the same station as the holotype are present at IRScN (Figures 3d–f): one of them is fairly well preserved and younger, the other is badly preserved.

The shell is ovate-elongate, not particularly convex, moderately robust, shortly rostrate, with a very shallow subrostral sinuation and an obscure posterior keel. The umbo is strongly opisthogyrate. The surface bears growth striae and ill defined, widely spaced commar-

Table 1
List of the type material.

	MOM	IRScN	MZR
<i>Leda excisa</i> var. <i>subexcisa</i>		5 vs	2 vs
<i>Leda bernardi</i>	1 v	2 vs	
<i>Leda mabiliei</i>	1 v		
<i>Leda allaudi</i>	1 v	1 v	
<i>Leda mirmidina</i>	2 vs	16 vs	
<i>Malletia pervieri</i>	1 v		

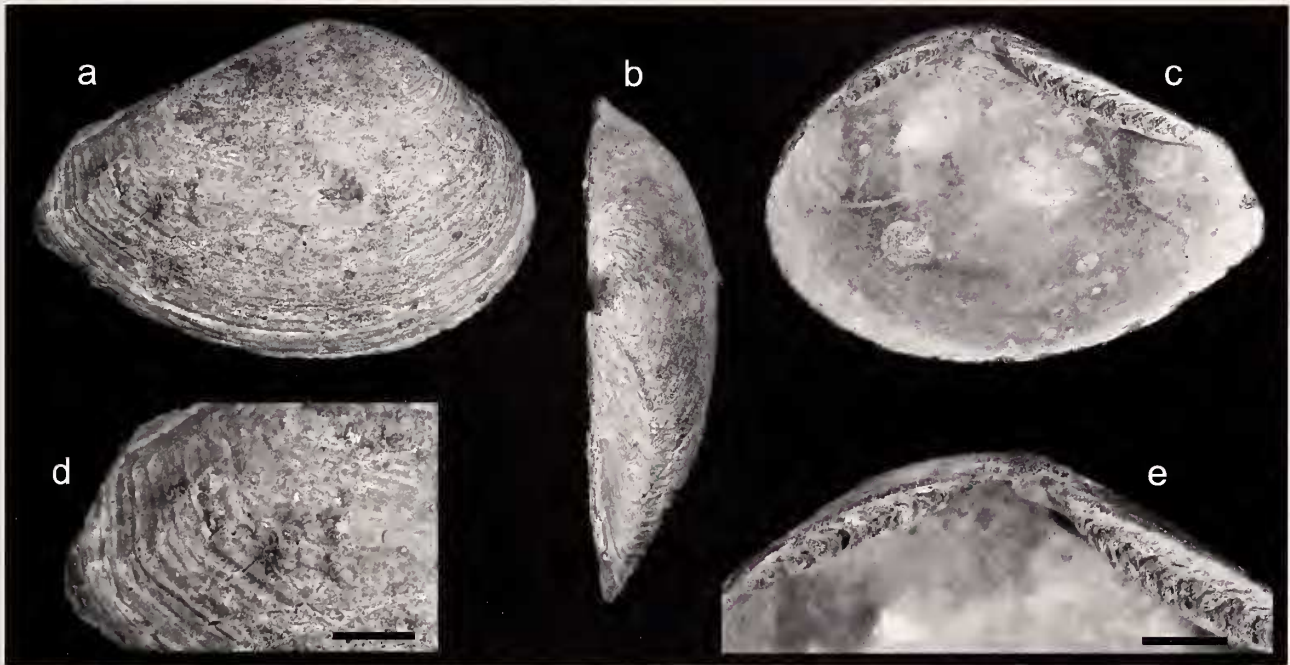


Figure 2. *Nuculana mabillei* (Dautzenberg & Fischer, 1897). a-e. Holotype (Dautzenberg & Fischer, 1897:pl. 6, figs 9, 10), length 10.35 mm, MOM 21160.

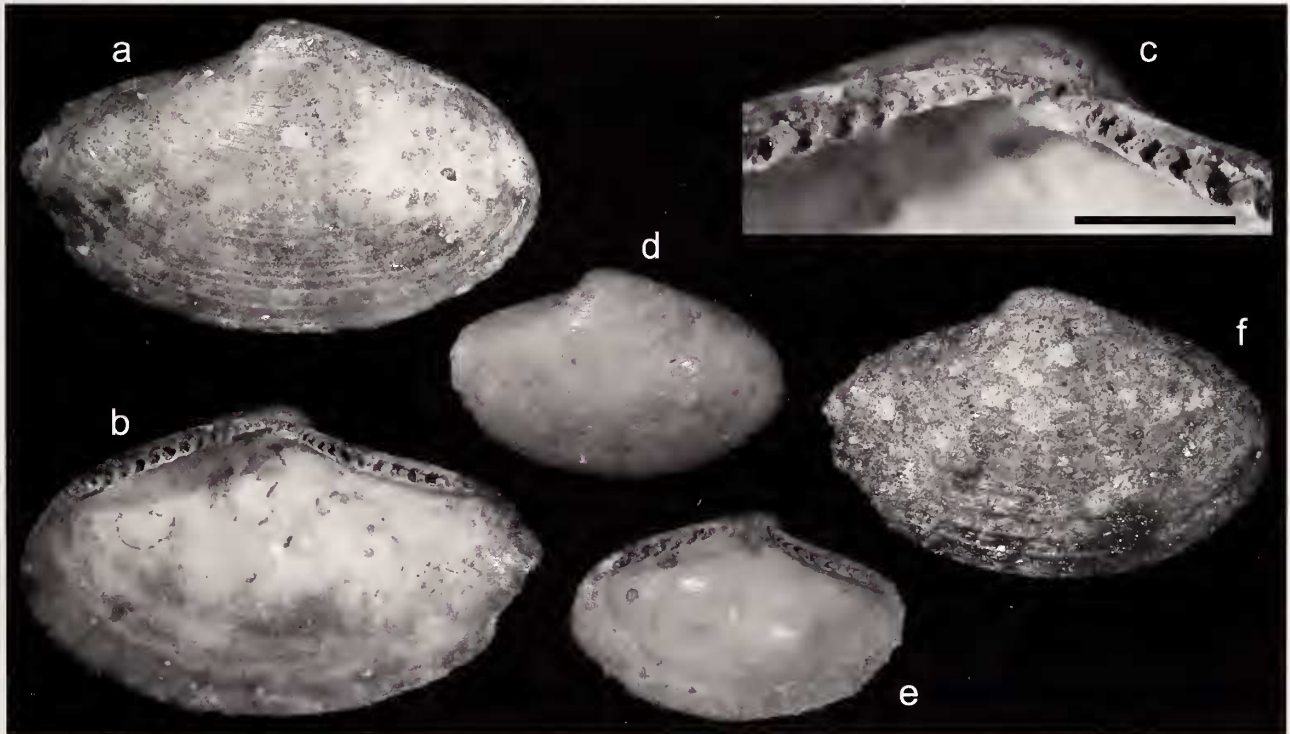


Figure 3. *Ledella bernardi* (Dautzenberg & Fischer, 1897). a-c. Holotype (Dautzenberg & Fischer, 1897:pl. 6, figs 5, 6), length 9.40 mm, scale bar = 1 mm, MOM 21158. d, e. topotype, length 6.11 mm, IRScN 1238. f. topotype, length 8.20 mm, IRScN 1238/5.

ginal ridges, becoming better defined near the ventral margin. The hinge is relatively strong, with a triangular, oblique ligament pit. The pallial sinus is well defined, not particularly deep. The larval shell is worn in all three valves.

This species shows remarkable similarities with a group of deep-water North Atlantic species which includes *Leda oxira* Dall, 1927, *Leda semen* Smith, 1885, *Ledella parva* Verrill & Bush, 1898 and *Ledella similis* Allen & Hannah, 1989. They share an ovate-elongate shell, a short rostrum, a poorly defined subrostral sinuation and a strongly opisthogyrate umbo. Of these, *Ledella similis* is the only species known from the West European Basin (Allen & Hannah, 1989), whereas *Leda oxira*, *L. semen* and *Ledella parva* are from the Western Atlantic (Smith, 1885; Verrill & Bush, 1898; Dall, 1927; Allen & Hannah, 1989). All of them were referred to *Ledella* by Allen & Hannah (1989) who also attempted to synonymise *Ledella parva* with *Leda semen* (see also Verrill & Bush, 1898). This problem is hard to resolve, since the type material of *Leda semen* is destroyed (Allen & Hannah, 1989), but the examination of the original illustrations (Smith, 1885:pl. 19, figs 2, 2a; Verrill & Bush, 1898:pl. 81, fig. 1) suggests a distinct status for both species. Another deep water species, *Ledella librata* Dell, 1952 from the Challenger Plateau, New Zealand, seems notably similar to the group of Atlantic species.

The systematic position of these species is not clear. They actually recall *Ledella*, but differ by being notably elongate and with a strongly opisthogyrate umbo. The species of *Ledella* usually have a rather sharp posterior keel, a well defined subrostral sinuation and a pointed rostrum (e.g., Warén, 1978; Allen & Hannah, 1989; La Perna et al., 2004). However, no other genus so far described seems to provide a better position for this group of species.

Genus *Yoldiella* Verrill & Bush, 1897

Yoldiella allaudi (Dautzenberg & Fischer, 1897)

(Figures 4a–d)

Leda allaudi Dautzenberg & Fischer, 1897:207, pl. 6, figs 7, 8.

Leda allaudi – Dautzenberg, 1927:290, pl. 8, figs 23, 24.
Nuculana allaudi – Clarke, 1962:52.

Types: Monaco exs., st. 703 (*Princesse-Alice* 1896, st. 74), 39°21'20"N, 31°06'W, 1360 m, 1 v, MOM 21156, lectotype; 1 v, IRScN, 1238/03, paralectotype.

Distribution: Only known from a single, deep water station, east of Flores, Azores. Other records (Daut-

zenberg & Fischer, 1897; Dautzenberg, 1927) cannot be confirmed.

Remarks: The shell of *Yoldiella allaudi* is delicate, markedly convex, ovate, distinctly inequilateral in shape and with a sculpture of thin, irregularly spaced commarginal ridges. The hinge is thin, with anterior and posterior rows of teeth of similar length, separated by a small, triangular ligament pit. The larval shell is ovate, 170 µm in maximum length.

The material of *Leda allaudi* at MOM consists of a single valve (st. 703), illustrated by Dautzenberg & Fischer (1897:pl. 6, figs 7, 8). Three valves from the same station are present at IRScN: one of them is *Leda allaudi*, whereas the two other valves belong to a new species herein described.

Additional material labelled as *Leda allaudi*, from two other stations, is present at IRScN: Monaco exs., st. 1349, 38°35'30"N, 28°05'45"W, 1250 m, Azores and st. 1114, 33°59'30"N, 8°12'45"W, 851 m, off Casablanca (Figure 1), but no specimen proves to be *Leda allaudi*. The material from the Azores includes 3 valves of an unidentified species, here kept as *Yoldiella* sp. A, and two poorly preserved, unidentifiable shells. The material from off Casablanca includes *Yoldiella semistriata* (Jeffreys, 1879) (2 vs, 1 sh), *Yoldiella seguenzae* Bonfitto & Sabelli, 1995 (2 vs) and an unidentified species (1 v), here kept as *Yoldiella* sp. B. Some of this material is illustrated in Figure 5.

In order to fix the identity of *Leda mabiliei*, a lectotype was designated (Figures 4a, b): it is the left valve from st. 703 (MOM), illustrated by Dautzenberg & Fischer (1897). The other valve from the same station at IRScN is a paralectotype (Figures 4c, d).

None of the many species of *Yoldiella* known from the Atlantic (e.g., Warén, 1989; Allen et al., 1995; Salas, 1996) seems particularly similar to *Y. allaudi*, except for *Y. subaequilatera* (Jeffreys, 1879) and the following new species, as discussed below.

Yoldiella dautzenbergi n. sp.

(Figures 4e–h)

Type material: Holotype and one paratype (left valves), IRScN, 1238/03.

Type locality: Monaco exs., st. 703 (*Princesse-Alice* 1896, st. 74), 39°21'20"N, 31°06'W, 1360 m.

Etymology: Named after Philippe Dautzenberg, Belgian malacologist (1849–1935).

Description: Shell small, thin walled, ovate, poorly elongate, subequilateral, moderately convex. Umbo at mid line, small, slightly opisthogyrate, distinctly protruding from shell outline. Posterior end well rounded, anterior end obscurely rostrate, slightly

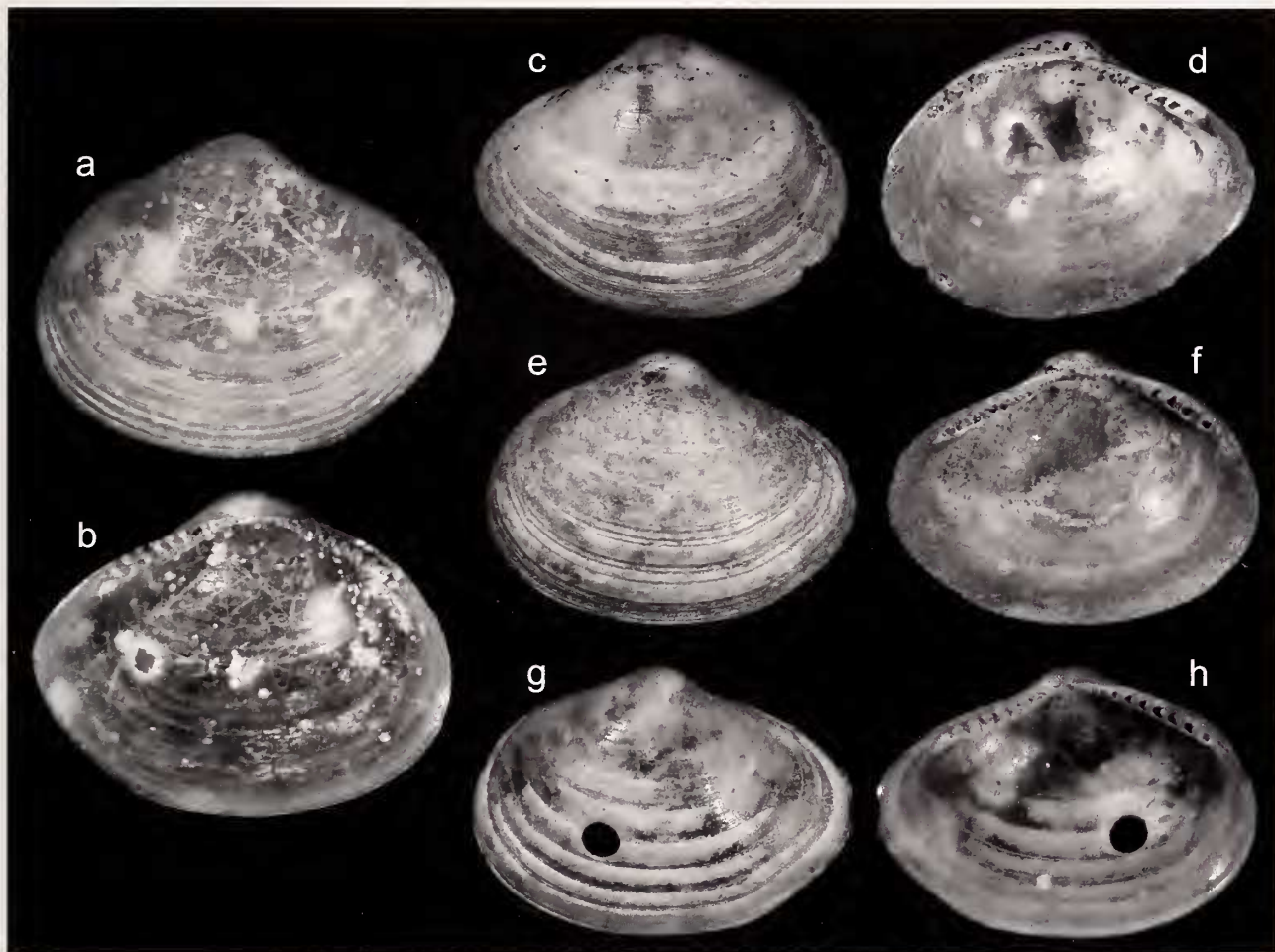


Figure 4. a–d. *Yoldiella allaudi* (Dautzenberg & Fischer, 1897). a, b Lectotype (Dautzenberg & Fischer, 1897:pl. 6, figs 7, 8), length 5.16, MOM 21156. c, d. Paralectotype, length 4.01 mm, IRScN 1238/03. e–h *Yoldiella dautzenbergi* n. sp. e, f. Holotype, length 4.02 mm, IRScN 1238/03. g, h. Paratype, length 4.08 mm, IRScN 1238/03.

narrower than anterior. Ventral margin moderately convex, with a faint slope break at postero-ventral transition. Subrostral sinuation almost absent. Sculpture consisting of growth striae and well incised, irregularly spaced commarginal lines, giving appearance of wide, flat ribs. Hinge plate thin, delicate. Dentition taxodont, with chevron-shaped teeth in two series of similar length, with about ten teeth anteriorly and posteriorly. Anterior row slightly convex, posterior row almost straight. Ligament pit small, triangular, sunken. Adductor muscle scars ovate, of similar size. Pallial sinus narrow, moderately deep. Prodissoconch ovate, 280 μ m in maximum diameter.

Measurements: holotype 4.02 mm in length, 2.97 mm in height, 1.05 mm in width; paratype 4.08 \times 2.90 \times 0.95 mm.

Distribution: Only known from a single, deep water station, east of Flores, Azores.

Remarks: The material of *Yoldiella dautzenbergi* n. sp. is from the lot of *Leda allaudi* at IRScN (see under *Yoldiella allaudi*).

Yoldiella dautzenbergi is much less convex, slightly less elongate and more equilateral than *Y. allaudi*, with the posterior end just slightly narrower than the anterior one. The umbo is less opisthogyrate and slightly smaller, the ventral margin less convex. In both species there is a faint slope break at the postero-ventral transition, but it is more distinct in *Y. dautzenbergi*. The subrostral sinuation is almost absent in *Y. dautzenbergi* and the sculpture consists of deeply incised, irregularly spaced commarginal lines, rather than of thin ridges. The larval shell is smaller than in *Y. allaudi*. The largest valve of *Y. allaudi* is about 5 mm in length, whereas the two valves of *Y. dautzenbergi* are about 4 mm, but the material is too scant for assessing a size difference between the two species.

A close resemblance also exists with *Yoldiella*

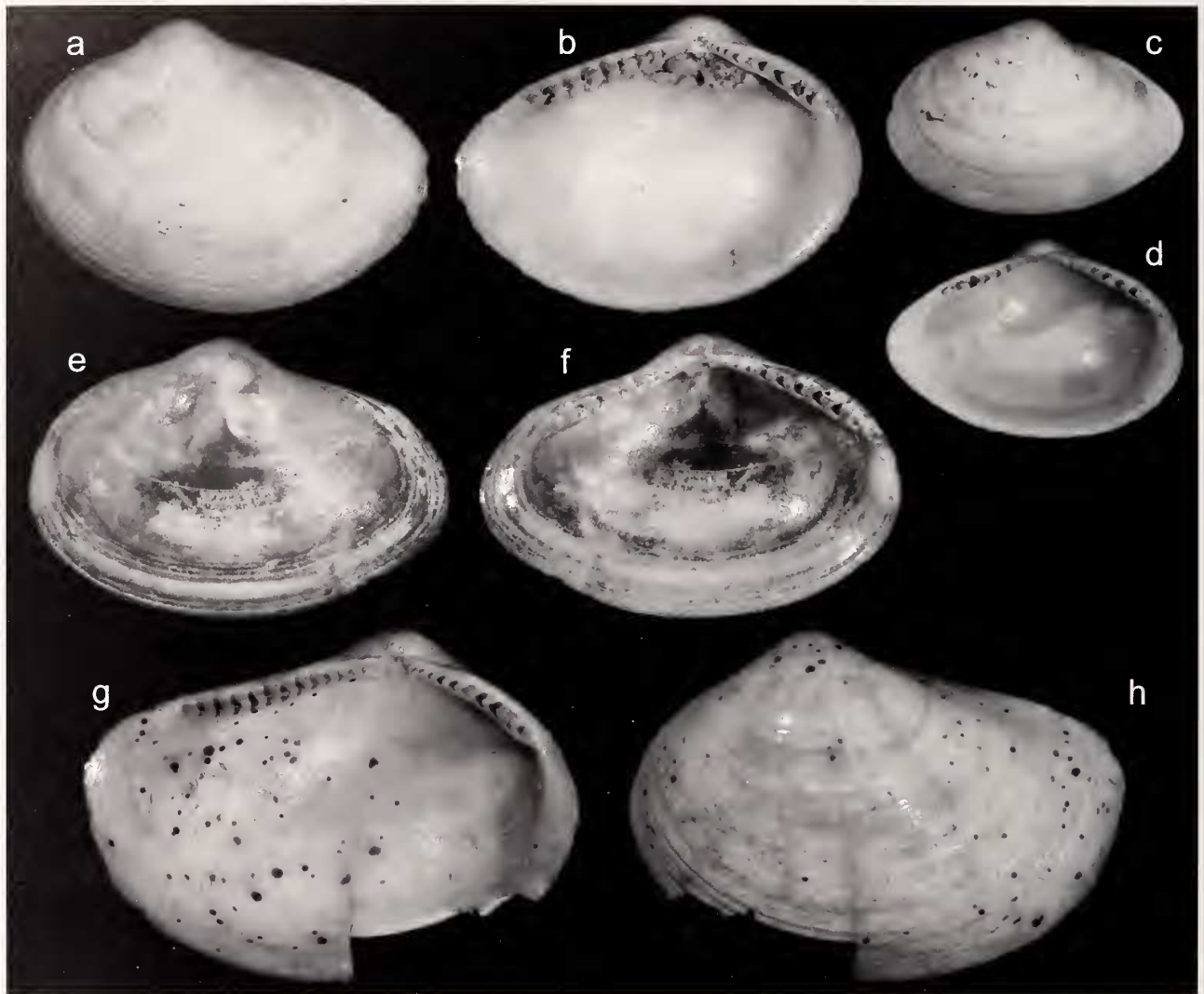


Figure 5. a, b. *Yoldiella semistriata* (Jeffreys, 1879). Monaco expeditions (1901), st. 1114, off Casablanca, length 3.56 mm, IRScN 1238/03. c, d. *Yoldiella seguenzae* Bonfitto & Sabelli, 1995. Monaco expeditions (1901), st. 1114, off Casablanca, length 2.58 mm, IRScN 1238/03. e, f. *Yoldiella* sp. A, Monaco expeditions (1902), st. 1349, Azores, length 3.62 mm, IRScN 1238/03. g, h. *Yoldiella* sp. B. Monaco expeditions (1901), st. 1114, off Casablanca, length 4.86 mm, IRScN 1238/03.

subaequilatera (Jeffreys, 1879), a poorly known deep water species from the Northeast Atlantic, dealt with by Warén (1989:p. 235, figs 10a, b). The new species is slightly less elongate and less equilateral than *Y. subaequilatera*, and more convex, with a narrower umbonal angle and with a better defined sculpture.

Genus *Microgloma* Sanders & Allen, 1973

Microgloma mirmidina (Dautzenberg & Fischer, 1897)

(Figures 6a–g)

Leda mirmidina Dautzenberg & Fischer, 1897:208, pl. 6, figs 11–14.

Leda mirmidina – Dautzenberg, 1927:292, pl. 8, figs 27–30.

Nuculana mirmidina – Clarke, 1962:53.

Types: Monaco exps., st. 698 (*Princesse-Alice* exp. 1986, st. 69), 1846 m, 39°11'N, 30°44'40"W, 2 vs, MOM 21157, syntypes; 16 vs, MIRScN 1239/02, syntypes.

Distribution: Only known from a single, deep water station, south-east of Flores, Azores.

Remarks: The position of the family Pristiglomidae Sanders & Allen, 1973 in the superfamily Nuculoidea, as proposed by Sanders & Allen (1973), was criticized by Ockelmann & Warén (1988) who assigned *Pristi-*

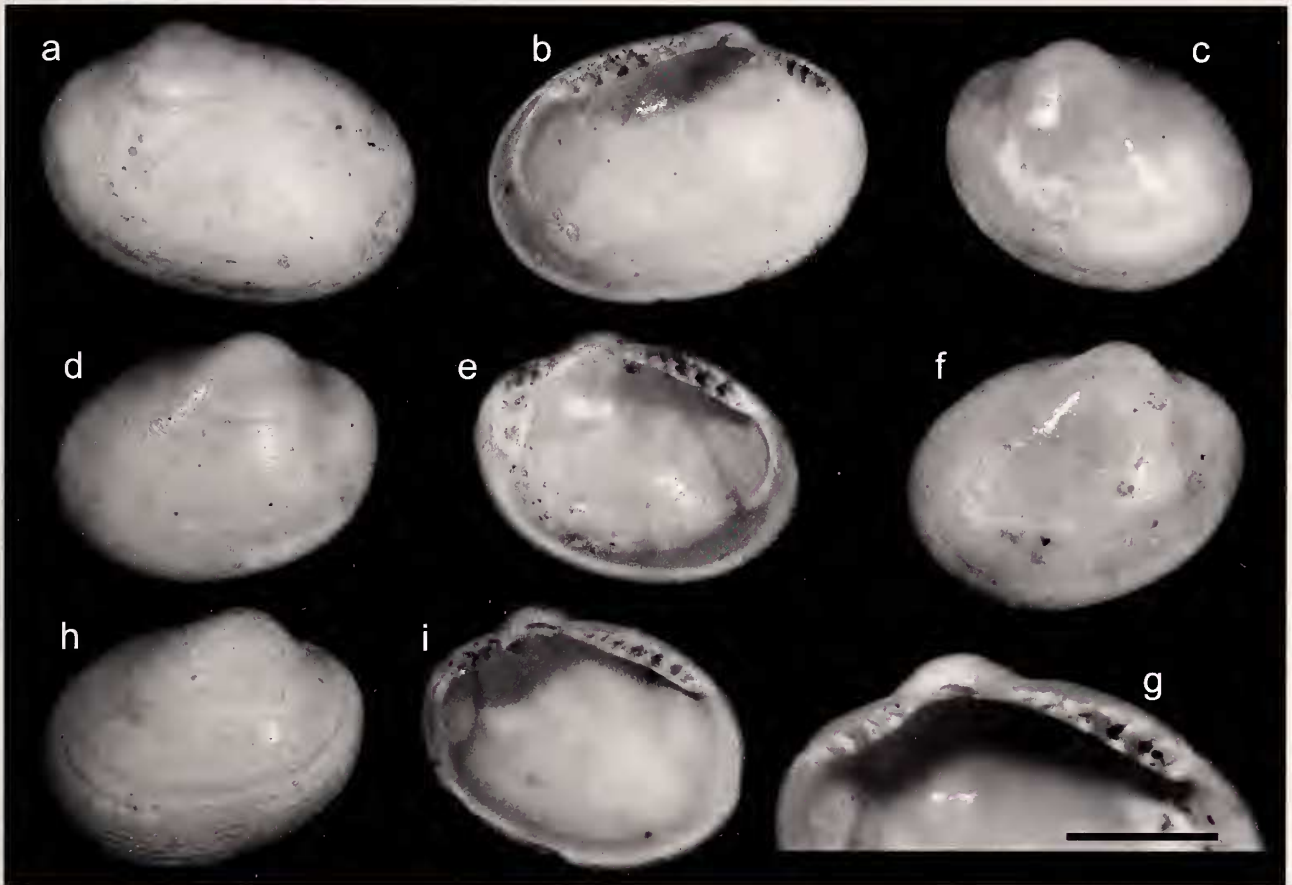


Figure 6. a–g. *Microgloma mirmidina* (Dautzenberg & Fischer, 1897). a, b. Syntype (Dautzenberg & Fischer, 1897:pl. 6, figs 12, 14), length 1.84 mm, IRScN 1239/02 (ligament pit enlarged by breaking or corrosion). c. Syntype, length 1.47 mm, IRScN 1239/02. d, e. Syntype, length 1.58 mm, IRScN 1239/02. f, g. Syntype, length 1.63 mm, scale bar =0.5 mm, IRScN 1239/02. h, i. Syntype, length 1.57 mm, MOM 21157.

gloma Dall, 1900 and *Microgloma* Sanders & Allen, 1973 to the Nuculanidae. They also presented strong evidence for the progenetic character of *Microgloma*.

Three further species of *Microgloma* were known, all from the Atlantic (Sanders & Allen, 1973; Ockelmann & Warén, 1998): *M. yongei* Sanders & Allen, 1973 (type species), *M. tumidula* (Monterosato, 1880) (= *M. turnerae* Sanders & Allen, 1973) and *M. pusilla* (Jeffreys, 1879). The last two species occur in European waters. Another European species, *Phaseolus guilonardi* Hoeksema, 1983 is provisionally placed in *Microgloma*, but it clearly belongs to a different group, as discussed by Ockelmann & Warén (1998) and La Perna (2003).

Microgloma mirmidina is somewhat similar to *M. yongei* and *M. tumidula* in the ovate-subrectangular shape, whereas *M. pusilla* is distinctly egg-shaped. All these species have a comparatively robust, notably convex shell, with a sculpture of thin ridges near the ventral margin. The muscle scars are slightly buttressed

in *M. mirmidina* and generally well-defined in the other species.

The largest syntype is 1.84 mm in shell length (Figures 6a, b), the others 1.5–1.6 mm. *Microgloma mirmidina* therefore is notably larger than *M. yongei*, *M. tumidula* and *M. pusilla* which are about 1 mm in shell length (Allen & Sanders, 1973; Ockelmann & Warén, 1998). The shell shape changes notably with growth, from dorso-posteroventrally oblique to posteriorly elongate, whereas the other species grow almost isometrically and equilaterally, as seen in the growth series of *M. yongei* and *M. tumidula* reported by Sanders & Allen (1973). This is probably due to the relatively large size of *M. mirmidina*, allowing this species to follow a growth pattern more similar to that of normal sized bivalves, whereas the other species are too small for manifesting marked allometric changes. At a size larger than 1.3–1.5 mm, the growth of *M. mirmidina* produces a stepped shell edge, giving a box-

like appearance. As observed by Ockelmann & Warén (1998), such a growth pattern which at a smaller extent occurs in the other species of *Microgloma*, provides an increase in shell volume and counterbalances the effects of miniaturization.

Besides the small size, Ockelmann & Warén (1998) remarked two other synapomorphies for the *Microgloma* species: the enlarged innermost teeth of the left valve and the radially wrinkled surface of the prodissoconch. The first character is not present in *M. mirmidina* (Figure 6g), but admittedly it is not always present or clearly developed in the other species (e.g., Ockelmann & Warén, 1998:fig. 9f). However, the hinge of *M. mirmidina* is similar to that of the congeners, with slightly chevron-shaped to rather stout teeth and a small, elongate ligament pit. The ligament pit is slightly oblique, with the anterior end apparently external or semi-external (Figure 6g). It is similar to the oblique ligament pit of a juvenile specimen of *Yoldiella philippiana* (Nyst, 1845) illustrated by Ockelmann & Warén (1998:fig. 3b), which differs by being posteriorly external. This supports the hypothesis by Ockelmann & Warén (1998:11) for the progenetic origin of *Microgloma* from *Yoldiella* or *Ledella*.

The larval shell of *M. mirmidina* is ovate, about 180 µm in length, notably smaller than that of *M. yongei* (290 µm) and *M. tumidula* (260–270 µm), more similar to that of *M. pusilla* (195–218 µm), according to the data by Sanders & Allen (1973) and Ockelmann & Warén (1998). Under optical magnification the prodissoconch surface shows an unresolved sculpture and it was not possible to ascertain if it corresponds to the radially wrinkled pattern reported by Ockelmann & Warén (1998).

Family Bathyspinulidae Coan & Scott, 1997

Genus *Bathyspinula* Filatova, 1958

Filatova & Shileyko (1984) pointed out the preoccupied status of *Spinula* Dall, 1908 by *Spinula* Herrich-Schaeffer, 1856 (Lepidoptera). They replaced the genus name *Spinula* with *Bathyspinula* Filatova, 1958, formerly subgenus of *Spinula*, and erected the new subgenus *Acutispinula*. Accordingly, *Bathyspinula* includes the subgenera *Bathyspinula* (*Bathyspinula*) and *B. (Acutispinula)*. Species of the latter differ by a finer, almost absent sculpture and a longer, sharper rostrum (Allen & Sanders, 1982; Filatova & Shileyko, 1984; Coan et al., 2000). The type species are *Bathyspinula (B.) oceanica* (Filatova, 1958) and *Bathyspinula (Acutispinula) calcar* (Dall, 1908), respectively.

Allen & Sanders (1982) erected the monogeneric subfamily Spinulinae (invalidly based on a junior homonym, replaced with Bathyspinulinae by Coan & Scott, 1997) in the family Nuculanidae to contain the genus *Bathyspinula*, whereas Filatova & Shileyko

(1984) included this genus in the subfamily Ledellinae, family Ledellidae Allen & Sanders, 1982. Ockelmann & Warén (1998) kept the Nuculanidae as a single, undivided family; a systematic view markedly different from the multi-taxa classification by Allen & Sanders (1986). However, as discussed below, there are good reasons for keeping *Bathyspinula* in a separate position, at a full family rank.

The adults of *Bathyspinula* possess a long, mainly external, amphidetic ligament, with a small internal component (Allen & Sanders, 1982; Di Geronimo & La Perna, 1996) (Figures 7a, b; see also the good illustrations by Knudsen, 1970). The internal ligament tends to a semi-external position and part of it can be seen externally, between the umbones of closed valves (Figure 7b). This condition is more evident in the juvenile stages, which possess a proportionally larger, clearly semi-external ligament pit (Figure 7c). The other nuculanids, such as *Nuculana*, *Ledella* and *Yoldiella* have a juvenile, external amphidetic ligament becoming fully internal with growth, as well-documented by Ockelmann & Warén (1998), or leaving a small external relict as in *Jupiteria* (La Perna et al., 2004). The ligament of *Bathyspinula* is then much more similar to that of the families Mallettiidae H. & A. Adams, 1858 (Sanders & Allen, 1985), Tindariidae Verrill & Bush, 1897 (Sanders & Allen, 1977) and Neilonellidae Shileyko, 1989 (Warén, 1989; Allen & Sanders, 1996; La Perna, 2007), all with a well-developed external ligament and a smaller internal component in the adults, than to that of the other nuculanids. None of these families provide a suitable position for *Bathyspinula*, for the following reasons: 1) mallettiids have a subrectangular, posteriorly truncate or bluntly rostrate, poorly sculptured shell; 2) neilonellids have an ovate, poorly rostrate shell with no trace of subrostral sulcus and postero-ventral sinuation; 3) tindariids have a roundish, not rostrate shell and are asiphonate (*Bathyspinula* has well developed, united siphons: Filatova & Shileyko, 1984; Allen & Sanders, 1982). A full family rank is therefore adopted for the Bathyspinulinae Coan & Scott, 1997 (= Spinulinae Allen & Sanders, 1982).

The family Bathyspinulidae also provides a suitable position for *Tindariopsis* Verrill & Bush, 1897, instead of the Tindariidae (Verrill & Bush, 1898), Mallettiidae (Dall, 1898; Vokes, 1980; Laghi, 1986) or even Nuculanidae, subfamily Ledellinae (Allen & Sanders, 1996). The type species, *Malletia (Tindaria) agathida* Dall, 1889 has the same ligament type as *Bathyspinula*, with a “well-marked dorsal ligamental furrow and a small notch or «socket» under the beak” (Verrill & Bush, 1897, 1898; see also Dall, 1898:582). *Tindariopsis agathida* has a shallow pallial sinus (Dall, 1898; Allen & Sanders, 1996) and cannot be assigned to the Tindariidae (which lack a pallial sinus), as suspected by Verrill & Bush (1898). On the other hand, the pointed, keeled

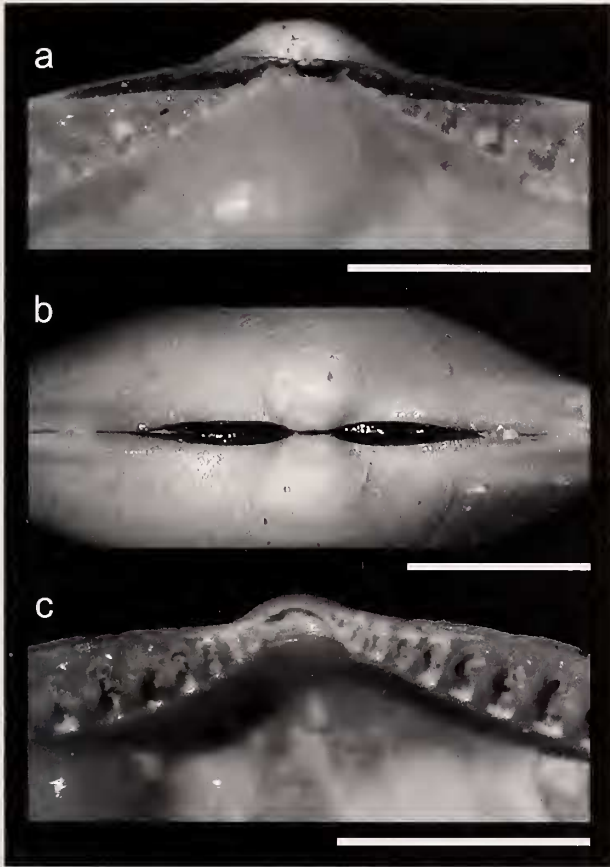


Figure 7. a–c. Ligament characters of *Bathyspinula*. a. *Bathyspinula subexcisa* (Dautzenberg & Fischer, 1897), Challenger exp. (1973), st. 4, length 5.01 mm, MCZ 348787. b. *Bathyspinula hilleri* (Allen & Sanders, 1982), st. DS23, length 4.93 mm, MCZ 348807. c. *Bathyspinula excisa* (Philippi, 1844), Archi, southern Calabria, Early-Middle Pleistocene, length 3.25 mm, author's coll. Scale bars: = 1 mm.

rostrum and the well-defined subrostral sulcus make *Tindariopsis* similar to *Bathyspinula* and markedly different from malletiids and neilonellids, whereas the resemblance with *Ledella* is due to convergence. A series of good illustrations, though with some misidentification, was published by Laghi (1986:pl. 8, figs 1a–6c; *Nuculana* cfr. *pusio* Philippi of figs 1a,b is a *Tindariopsis* species), including the holotype of *Tindariopsis agathida*.

Bathyspinula (*B.*) *subexcisa* (Dautzenberg & Fischer, 1897)

(Figures 7a, 8a–k, r, s)

Leda excisa var. *subexcisa* Dautzenbeg & Fischer, 1897: 205.

Leda (*Neilo*) *excisa* var. *subexcisa* – Dautzenberg, 1927:295.

Spinula subexcisa – Clarke, 1962:52 (?).

Spinula subexcisa – Allen & Sanders, 1982:21, figs 22, 23, 27, 28.

Types: Monaco exps., st. 698 (*Princesse-Alice* 1896, st. 69), 39°11'N, 30°44'40"W, 1846 m, Azores, 5 vs, IRScN 1238/01, syntypes; Monterosato coll., 2 vs, MZR 14423, syntypes.

Other material examined: Challenger exp. (1973), st. 4, 56°52'N, 10°01'W, 1993 m, Rockall Trough, 4 shs, 1 v, MCZ 348787 (Allen & Sanders, 1982). Chain 106 exp. (1972), st. 318, 50°26.8'–50°27.3'N, 13°19.9'–13°20.9'W, 2506 m, off West Ireland, 5 shs, MCZ 348785.

Distribution: *Bathyspinula subexcisa* is known from the North Atlantic (West Europe and Azores), in 1846–2506 m.

Remarks: The history of *Bathyspinula subexcisa* is closely linked to *Nucula excisa* Philippi, 1844, described from the Plio-Pleistocene of Southern Italy (Philippi, 1844: p. 46, pl. 15, fig. 4; Di Geronimo & La Perna, 1996). According to Allen & Sanders (1982), the records of *Malletia excisa* by Jeffreys (1876, 1879) and of *Leda excisa* by Smith (1885) from the North Atlantic could have been based either on *Bathyspinula subexcisa* or on *Bathyspinula hilleri* Allen & Sanders, 1982, both occurring in the North Atlantic, the latter with a much wider Atlantic distribution. Also the record of *Spinula subexcisa* from the South Atlantic by Clarke (1961) was probably based on a different species, possibly *Bathyspinula hilleri*. He compared his specimens with material from the Jeffreys coll. and found them “identical to *M. excisa*, as Jeffreys understood it.”

This is the first time the type material of *Bathyspinula subexcisa* is revised. The sole illustrations so far available for this species were the drawings by Allen & Sanders (1982).

The most obvious differences from *Bathyspinula excisa* (Figures 8n–q) lie in the shallower subrostral sinus and in the finer sculpture. *Bathyspinula subexcisa* also differs by being less convex and more delicate, with a shorter rostrum and a less distinct rostral keel.

Allen & Sanders (1982) reported *Bathyspinula subexcisa* from a single station (Challenger exp. 1973, st. 4). Some of this material was examined (Figures 8f–i) and it actually matches the type material. Microscopic, anastomosing radiating lines, are present along the subrostral sulcus; they are similar to the microsculpture present in *Bathyspinula excisa* (Di Geronimo & La Perna, 1996:pl. 2, figs 1, 1a). This character is not visible in the type material of *B. subexcisa*, most probably due to the poor preservation. Other specimens (Chain 106 exp. 1972, st. 318) differ by having a

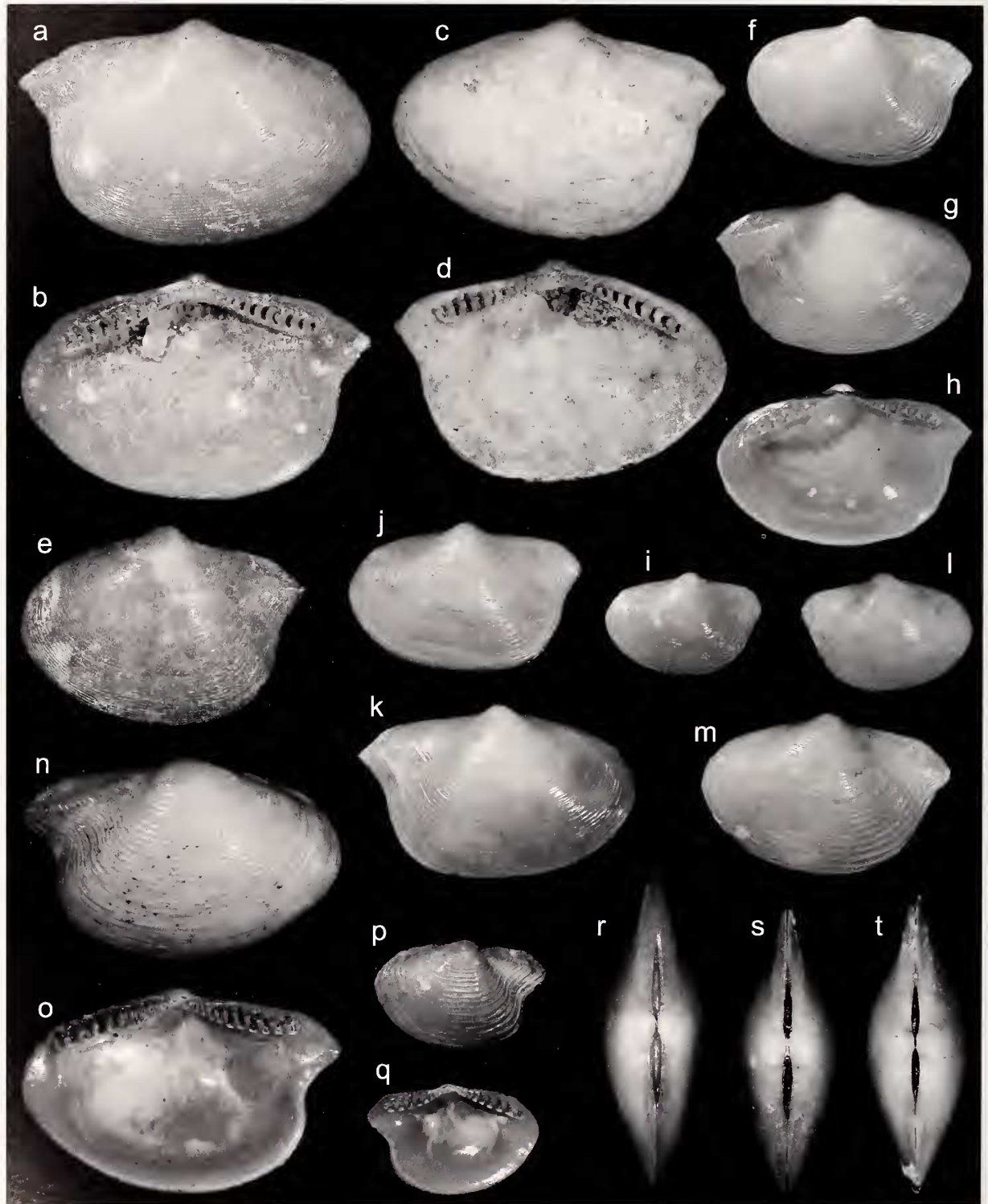


Figure 8. a–k. *Bathyspinula subexcisa* (Dautzenberg & Fischer, 1897). a, b. Syntype, length 6.81 mm, IRScN 1238/01. c, d. Syntype, length 6.52 mm, IRScN 1238/01. e. Syntype, length 5.47 mm, IRScN 1238/01. f. Challenger exp. (1973), st. 4, length 4.44 mm, MCZ 348787. g, h. Challenger exp. (1973), st. 4, length 5.01 mm, MCZ 348787. i. Challenger exp. (1973), st. 4, length 3.09 mm, MCZ 348787. j. Chain 106 exp., st. 318, length 4.42 mm, MCZ 348785. k. Chain 106 exp., st. 318, length 5.35 mm, MCZ 348785. l, m. *Bathyspinula hilleri* (Allen & Sanders, 1982). l. St. DS23, length 3.42 mm, MCZ 348807. m. St. DS23, length 4.93 mm,

less convex ventral margin (Figures 8j, k), but apparently without any clear-cut separation from the specimens with a more convex ventral margin.

The larval shell of *B. subexcisa* is ovate, similar in size and shape to that of *B. excisa* (Di Geronimo & La Perna, 1996:pl. 2, fig. 3), 280–300 µm in length, both in the type material and in the material from MCZ. This contrasts with the size of 450 µm reported by Allen & Sanders (1982:23): such a difference must be due to a measurement error.

Bathyspinula hilleri was described from the Angola Basin and reported from a number of stations through the Atlantic Ocean (Allen & Sanders, 1982). Some material (Figures 8m, t) from the West European Basin (st. DS23, 46°32.8'N, 10°21'W, no data on cruise and station depth, not reported by Allen & Sanders, 1982, tab. 4), matches the original description. It differs from *Bathyspinula subexcisa* by having a more convex ventral margin, a slightly coarser sculpture, particularly near the ventral margin, and by being slightly more inflated.

Bathyspinula excisa is notably common in the Plio-Pleistocene bathyal deposits cropping out in Italy (Di Geronimo & La Perna, 1996, 1997; La Perna, 2003). The finding of a single, fresh valve in the Ibero-Moroccan Gulf (Salas, 1996) seems to bring evidence that small populations are still present in the adjacent Atlantic. The depth range of *Bathyspinula excisa* was (or is) much shallower, from 200–300 m down to some 1000 m at least, than that of *B. subexcisa* and the other congeners, greatly exceeding 1000 m (Knudsen, 1970; Allen & Sanders, 1997; Olabarria, 2005).

Family Tindariidae Verrill & Bush, 1897

Genus *Tindaria* Bellardi, 1875

Tindaria perrieri (Dautzenberg & Fischer, 1897)

(Figures 9a–c)

Malletia perrieri Dautzenberg & Fischer, 1897:208, pl. 6, figs 15, 16.

Malletia perrieri var. *curta* Locard, 1898:333, pl. 18, figs 20–24.

Malletia perrieri – Dautzenberg, 1927:296, pl. 8, figs 19, 20.

Types: Monaco exs., st. 698 (*Princesse-Alice* 1896, st. 69), 39°11'N, 30°44'40"W, 1846 m, 1 v, MOM 21159, holotype.

Distribution: Azores (south-east of Flores) and North-west Africa (off Rabat), 1846–2190 m.

Remarks: The holotype is a poorly preserved right valve, somewhat robust, ovate in shape, with anterior and posterior ends well rounded and a strongly anterior umbo. Most of the outer surface bears only growth striae and ill-defined commarginal ridges, becoming better defined, sharper and regularly spaced towards the ventral margin. The hinge is moderately strong, arched with a continuous series of teeth. As observed by Dautzenberg & Fischer (1897), there is no ligament pit. A thin, barely visible external ligament furrow is present posteriorly, slightly extending anteriorly.

Malletia perrieri var. *curta*, described by Locard (1898) from the *Talisman* st. 16, 2190 m, off Rabat, Morocco (the original coordinates were based on the Paris meridian and the corrected version is 34°01'N, 08°32'W; S. Gofas, pers. comm.) is a synonym of *Malletia perrieri*. This is supported by the close matching of the two descriptions and the almost perfect overlap of the shell outlines. Locard's var. *curta* was said to be slightly higher and shorter, but the two original valves (of the same shell, as inferred from the illustrations) are only slightly larger, 9 mm in length, 8 mm in height, than the holotype of *Malletia perrieri* (7.93 × 6.92 mm), with the same length to height ratio.

According to Sanders & Allen (1977), *Tindaria* Bellardi, 1875 and *Pseudotindaria* Sanders & Allen, 1977 (currently in the Neilonellidae) cannot be distinguished from each other conchologically (*Pseudotindaria* differs from *Tindaria* by having siphons). Warén (1989) remarked that *Pseudotindaria* has an edentulous gap in the hinge, as in the type species *Pseudotindaria erebus* (Clarke, 1959). This observation seems more useful for distinguishing the two genera than the assumption by Maxwell (1988) that *Tindaria* lacks a pallial sinus. The type species of *Tindaria* is *T. arata* Bellardi, 1875, from the Late Miocene of the Turin area. The examination of the types and of abundant topotypic material of *T. arata* confirmed Warén's (1989:255, figs 19c, d) observations: 1) the tooth series is continuous (more precisely, there is a short interruption, sometimes poorly defined, much shorter than the edentulous gap in *Pseudotindaria*); 2) the pallial line is feeble, slightly distinct anteriorly, fading posteriorly and, apparently, without sinus.

The characters of *Malletia perrieri* all point to *Tindaria* (except for the inability to examine the pallial

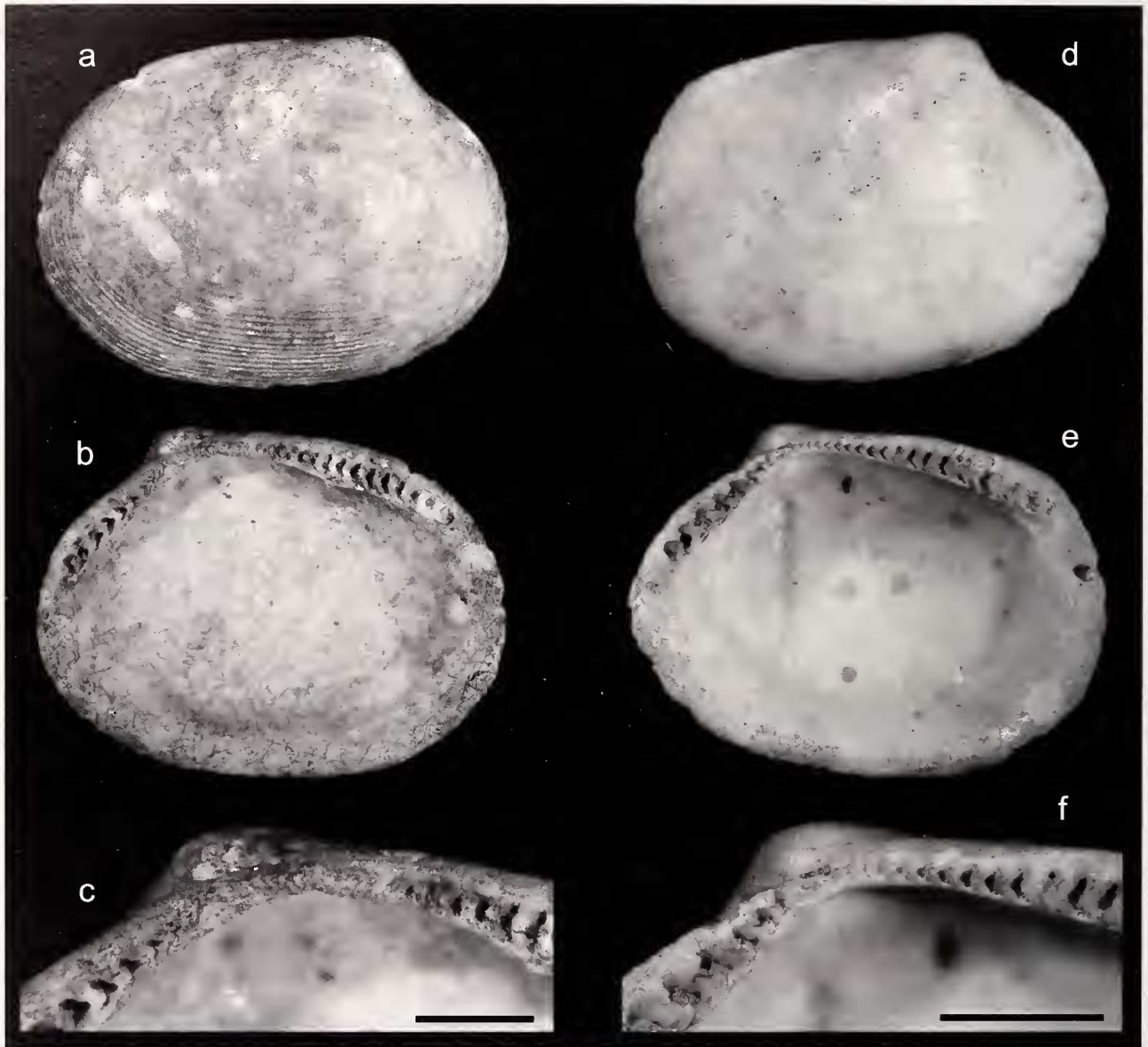


Figure 9. a–c. *Tindaria perrieri* (Dautzenberg & Fischer, 1897), holotype (Dautzenberg & Fischer, 1897:pl. 6, figs 15, 16), length 7.93 mm. MOM 21159. d–f. *Tindaria* sp., length 5.96 mm, IRScN 1238/4. Scale bars = 1 mm.

line because of the poor preservation status). None of the Atlantic tindariids (Sanders & Allen, 1977; Warén, 1989) seems particularly similar to *Tindaria perrieri*.

A single right valve labelled as *Malletia perrieri* is present at IRScN (Figures 9d–f), from the same station as the holotype at MOM. No mention of this valve was made, either by Dautzenberg & Fisher (1897) or by Dautzenberg (1927). It is rather robust, not markedly convex, with a sculpture of only growth striae. The posterior margin is poorly convex or somewhat truncate, with a slope break at the postero-dorsal transition. An external ligament furrow is present

posteriorly. The pallial line is somewhat straight posteriorly, with no pallial sinus. It seems to represent an undescribed species, of uncertain systematic position, provisionally kept as *Tindaria* sp.

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